

1160 W. Orange Grove Ave., Arcadia, California, U.S.A. 91006
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NOTE ON DAMAGED SPECIMENS

JOHN M. KOLYER

55 Chimney Ridge Drive, Convent, New Jersey 07961, U.S.A.

IT IS INTERESTING to note the extent to which butterflies may be damaged and yet remain capable of normal flight. This note presents measurements on a few specimens with severe wing damage and discusses these with reference to some of the pertinent literature.

ATTACKS BY BIRDS

There is considerable debate in the literature regarding bird attacks, the interest being in supporting or discounting Batesian mimicry. For example, Wheeler (1935) concludes that attacks on flying butterflies are very rare and that most insectivorous birds are incapable of capturing uninjured butterflies in flight. This is stated to lead to the conclusion that "the current theory of mimicry as applied to the upper wing colors of butterflies is unsound". However, a considerable number (262) eyewitness accounts of bird attacks compiled by Collenette (1935) showed that 17% of the butterflies were captured at rest and 83% in flight. Of course, it is recognized that in-flight attacks are the more conspicuous, so that the only valid conclusion is that in-flight captures are not uncommon.

Collenette (1935) also notes that symmetrical damage, as in specimens 1 and 4 in the figure, strongly indicates a bird attack, probably while the insect was at rest rather than with wings momentarily together in flight. Carpenter (1942) examined 14,000 specimens for beak marks on the wings and concluded that the small percentage of beak-marked specimens evidently attacked at rest (symmetrical damage) militates against the view that butterflies usually are attacked at rest. Therefore, it follows that mimicry on the upper surface *would* be perceived by birds. This conclusion is in disagreement with Wheeler's belief

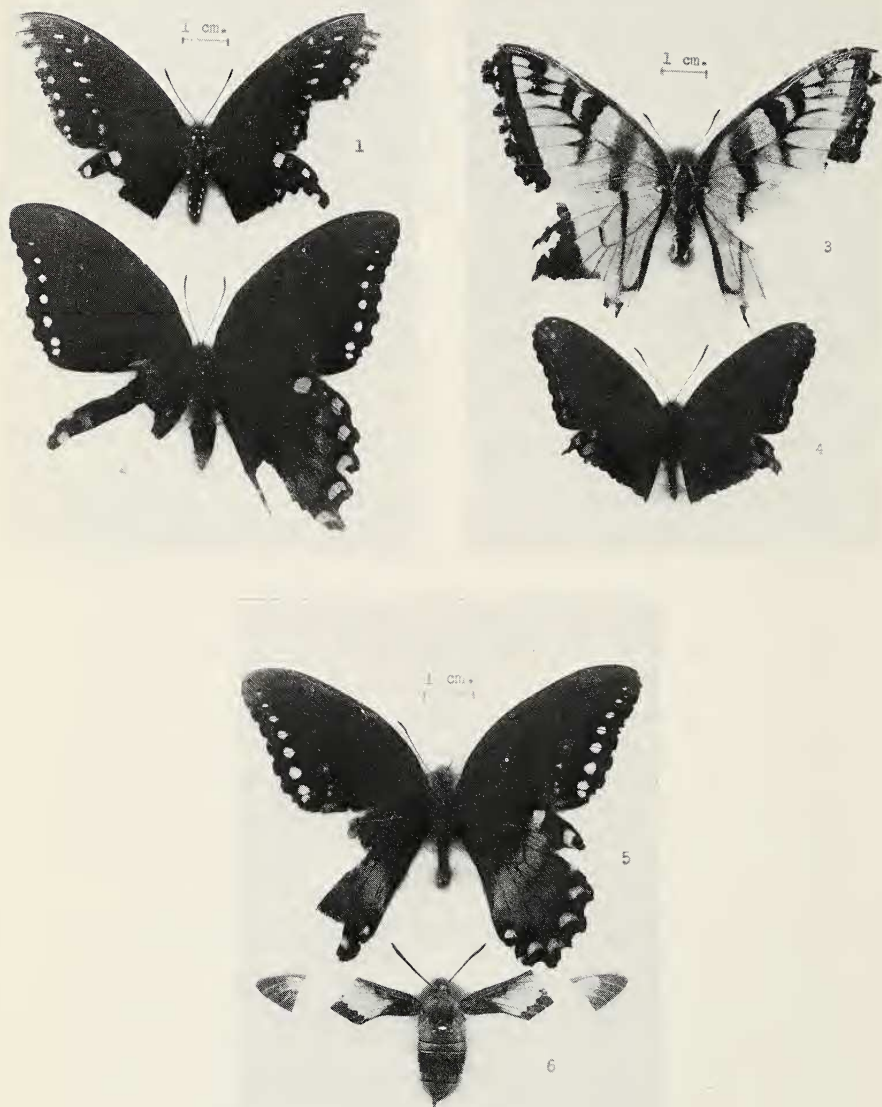


Fig. 1

All specimens were taken near Morristown, New Jersey and were flying strongly when captured. 1 — *Papilio polyxenes asterius* Stoll, ♀, taken Aug. 6, 1966. 2 — *Papilio troilus* Linnaeus, ♀, taken Aug. 6, 1966. 3 — *Papilio glaucus* Linnaeus, ♂, taken Aug. 30, 1967. 4 — *Limenitis arthemis astyanax* Fabricius, ♂, taken July 30, 1966. 5 — *Papilio troilus* Linnaeus, ♂, taken Aug. 12, 1966. 6 — *Hemaris thysbe*, taken Aug. 7, 1966.

that attacks on flying butterflies are rare but does no more than remove one objection to the theory of upper-surface mimicry. Incidentally, a recent criticism of the common mimicry theory, e.g. the Monarch-Viceroy relationship, is given by Urquhart (1960).

An interesting conclusion by Carpenter (1942) is that attacks by birds upon butterflies are predominantly (about 55% of cases studied) from behind and less often from in front (about 30%) or from the side (about 15%). Specimen 2 in the figure shows what seem to be beak marks on the hind wings, while specimens 3 and 5 show considerable tearing; according to Collentte (1935) the majority of butterflies after being captured by birds show torn wings rather than clear beak marks. However, as Collentte notes, unless the attack is seen, torn wings cannot be ascribed to bird attacks with any degree of confidence.

Thus, specimens 1-5 seem to illustrate two cases of bird attacks from the rear while at rest (specimen 4, which is clipped very cleanly, and specimen 1), one case of bird attack(s) from behind in flight (specimen 2), and two other possible cases of attacks in flight (specimens 3 and 5).

EFFECT OF DAMAGE ON FLIGHT

The wing areas for the specimens in the figure were determined by inking the outline of the wings on clear plastic sheet (0.042 inch thick), cutting along the lines, and weighing the tracings with an analytical balance. The areas for undamaged fore- and hindwings were determined similarly by consulting undamaged specimens. The extents of wing areas remaining then were calculated and are given in Table 1. Since all of specimens 1-5 were flying vigorously and apparently going about their usual activities, a considerable part of the wing area (32% for specimen 1) seems to be expendable, at least when removed largely from the hindwings.

Static loads (weight of insect divided by wing area) have been recorded for various insects; examples (experimentally determined and from the literature) are given in Table 2. The experimental determinations are based on weights of freshly-killed specimens.

Assuming the static load to be about 0.009 g./cm.² for an undamaged *Papilio polyxenes asterius* Stoll female, damage has raised the load to 0.013 g./cm.² for specimen 1, an increase of about 47% (neglecting weight of wing membrane lost).

Table 1

EXTENTS OF DAMAGE FOR SPECIMENS 1-5

Specimen No.	Forewing, P. C. Area Retained			Hindwing, P. C. Area Retained			Total Area, P. C. Retained
	Left	Right	Both	Left	Right	Both	
1	96	83	89	43	50	47	68
2	99	100	100	28	83	56	78
3	94	87	91	64	41	53	72
4	100	100	100	54	59	57	79
5	100	100	100	55	95	75	88

P. C. = per cent

Table 2

STATIC LOADS

Item	Static Load, g./cm. ²	Reference
<u>Papilio glausus</u> Linnaeus (male)	0.0093	
<u>Papilio troilus</u> Linnaeus (male)	0.0081	
<u>Cercyonis pegala</u> Fabricius	0.0063	
<u>Colias eurytheme</u> Boisduval (male)	0.011	
<u>Hemaris thysbe</u>	0.10	
Papilionids and pierids	approx. 0.01	Portier, 1949
Butterflies in general	0.01 - 0.015	Portier and de Rorthays, 1926
<u>Bombus</u> (Bombidae)	0.25	" "
Monoplanes, circa 1926	1.3 - 2.3	" "
Aircraft, circa 1953	7.5 - 40	Chadwick, 1953

The following simple experiments give some idea of the extent of wing loss that can be tolerated and of the relative importance of forewings vs. hindwings.

Hemaris thysbe. — Complete removal of the hindwings (37% of total wing area) had no apparent effect on flight, but removal of the apices of the forewings (comprising about 32% of the forewing area), as shown in the figure (specimen 6), resulted in slanting flight, perhaps 30° from the horizontal, toward the floor.

Limenitis archippus Cramer. — After removal of the apices of the forewings to the extent of 53% of the forewing area (27% of total wing area), a specimen still was capable of level flight for 10 feet. The wingbeats seemed faster, as has been noted for insects when the wing area is reduced (Chadwick, 1953). When the hindwings (49% of total area) were quite removed, another specimen flew well but somewhat erratically. Then, removal of the apices of the same specimen to the extent of 20% of the forewing area caused even more erratic flight, but level flight for 10 feet was achieved. The forewings (51% of total wing area; forewings are 50-56% of the total for the four species of specimens 1-5, incidentally) were quite removed from another specimen. Complete inability to fly resulted, and the insect was unable to rise above an inch from the floor. Thus, level flight is possible using 80% of the forewings when the hindwings are missing, but no flight is possible using 100% of the hindwings when the forewings are absent.

Colias philodice Latreille. — As with the Viceroy, complete removal of the hindwings (51% of total wing area) from a male specimen caused flight to be rather erratic, but the specimen could sustain flight for at least one minute and was able to fly across a 25 foot room and readily direct itself to a small (about 1 ft.²) window.

Papilio glaucus Linnaeus. — To test the effect of unsymmetrical damage, even more extreme than for specimen 5 in the figure, one hind wing (25% of total wing area) was removed from an undamaged female. Flight was not noticeably impaired.

CONCLUSION

In the Lepidoptera, the hindwings are said to associate closely with the forewings to yield a single aerodynamic unit (Chadwick, 1953). However, though the wing area is about equally divided between fore- and hindwings for the butterfly species studied above, the forewings are dominant so that a limited part

of the forewing area seems expendable vs. a major part of the hindwings. Fortunately, attacks by birds tend to come from the rear. Also, unsymmetrical damage can be tolerated, and in-flight bird attacks, perhaps very common, tend to damage the wings on one side more than the other (e.g., specimens 2, 3, and 5 in the figure).

It seems possible that the large wings of some butterflies are a rather neutral factor in regard to survival of bird attacks. That is, butterflies may be more conspicuous to birds than are bees, for example, but an increase in relative frequency of attacks may be balanced by reduced relative frequency of success in that birds tend to peck at the partly-expendable wings (especially the hindwings) and miss the body. It might even be hypothesized that the hindwings of certain species, for example *Papilio troilus* Linnaeus, which are conspicuously marked and tailed, are of survival value in causing birds to peck at the most-expendable part of the insect. Also, in many species the margins (expendable) of both fore- and hindwings often are decorated conspicuously.

This idea, like Batesian mimicry, might be most difficult to demonstrate convincingly. Urquhart (1960) notes that bright white tags applied to the wings of Monarchs seemed to attract the attention of birds. A possible (though perhaps not practical) experiment would be to apply white tags to various parts of the wings of a large number of individuals of a suitable species of butterfly and release these in a roomy aviary along with insectivorous birds. To support the above idea, significantly more specimens with tags on the hindwings and/or margins of the wings should survive (remain in flying condition) than those marked with tags on the inner parts of the forewings. A likely result, of course, is that the birds might not be capable of enough accuracy to strike at the particular part of the wing surface with the tag. This would give survival rates independent of tag position and tend to discount the survival value of conspicuous markings on the more-expendable areas of the wings, at least for the particular bird species involved.

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